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Extrapolating population size from the occupancy–abundance relationship and the scaling pattern of occupancy

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Abstract. The estimation of species abundances at regional scales requires a cost-efficient method that can be applied to existing broadscale data. We compared the performance of eight models for estimating species abundance and community structure from presence–absence maps of the southern African avifauna. Six models were based on the intraspecific occupancy–abundance relationship (OAR); the other two on the scaling pattern of species occupancy (SPO), which quantifies the decline in species range size when measured across progressively finer scales. The performance of these models was examined using five tests: the first three compared the predicted community structure against well-documented macroecological patterns; the final two compared published abundance estimates for rare species and the total regional abundance estimate against predicted abundances. Approximately two billion birds were estimated as occurring in South Africa, Lesotho, and Swaziland. SPO models outperformed the OAR models, due to OAR models assuming environmental homogeneity and yielding scale-dependent estimates. Therefore, OAR models should only be applied across small, homogenous areas. By contrast, SPO models are suitable for data at larger spatial scales because they are based on the scale dependence of species range size and incorporate environmental heterogeneity (assuming fractal habitat structure or performing a Bayesian estimate of occupancy). Therefore, SPO models are recommended for assemblage-scale regional abundance estimation based on spatially explicit presence–absence data.

Key words: abundance estimate; avifauna of South Africa, Lesotho, and Swaziland; occupancy–abundance relationship; presence–absence map; scaling patterns of occupancy; spatial scales.

Introduction

Abundance is one of the most important measures of species conservation status (IUCN 2001) and a surrogate for ecological functioning (Gaston and Blackburn 2000, McGill et al. 2007). Estimates of species abundances can aid the understanding of community structure (e.g., constructing abundance-rank curve; Gaston and Blackburn 2000), improve the monitoring of changes in biodiversity (Wilson et al. 2004), and optimize conservation efficiency (Reyers et al. 2007). Therefore, any efficient technique for estimating abundances across entire species assemblages is useful for biodiversity conservation, especially given anthropogenic global environmental change (Channell and Lomolino 2000, Brook et al. 2008).

Various experimental and mensurate methods have been used to estimate species abundances. However, complete counts and techniques such as mark–recapture and indirect counts (Blower et al. 1981, Seber 2002) are only useful for local abundance estimates due to the small scales at which data can be collected. As a result, much attention has been paid to the abundance of rare and/or localized species, such as endangered and flagship species (e.g., Simberloff 1998, Andelman and Fagan 2000). These techniques cannot be used at regional scales because the data required for calculating abundance (e.g., capture–release data for the mark–recapture method) are not available at such broad spatial scales. Consequently, species abundance across its entire distribution range is often incalculable, especially for common species (Gaston 2008).

Binary (presence/absence) data are now available at broad spatial scales for many species. These data are cost efficient to collect (Brotons et al. 2004, Joseph et al. 2006) and are available for a diversity of taxa at continental and global scales (e.g., vertebrates, selected invertebrate and plant groups). Two categories of abundance estimation models have been developed that use such binary data. The first, the intraspecific occupancy–abundance relationship (OAR hereafter; He and Gaston 2000, 2003) is grounded in the ubiquitous positive intraspecific correlation between abundance and range

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TABLE 1. Summary of the tests and the criteria of the dipswitch test, by two classes of tests, for the six occupancy–abundance relationship (OAR) models and the two scaling pattern of occupancy (SPO) models.

	OAR models‡						SPO models§	
Test and criteria†	PSN	MTP	EXP	NBD	GNBD	INBD	LLM	BEM
Macroecological patterns								
Species abundance distribution								
Smoothness of the rank–abundance curve	+	−	−	+	−	−	+	+
Log-normal shape	−	−	−	+	−	−	+	+
Left-skewed	+	−	−	+	+	+	+	+
Occupancy–abundance relationship								
Significantly related	+	+	+	+	−	−	+	+
Slope compared to British birds[1]	−	−	−	+	−	−	−	−
Slope compared to observed data[2]	−	−	−	−	−	−	+	−
Abundance–body mass relationship								
Significantly related	−	−	+	+	+	+	+	+
Slope compared to Australian birds[3]	−	−	−	−	−	+	+	+
Slope compared to −0.75[4]	−	−	−	−	−	+	+	+
Slope compared to observed data[2]	−	−	−	−	−	+	+	+
Comparison to published abundance estimates								
Rare species								
Significantly related	−	+	−	−	−	−	+	+
Explained deviance >10%	−	+	−	−	−	−	−	+
AIC weight	−	−	−	−	−	−	−	+
Estimation–observation slope against unity	+	+	−	−	−	−	−	−
Total regional abundance estimate								
$1–9 \times 10^9$ individuals	−	−	−	−	−	−	+	+

† References for criteria: 1, Holt and Gaston 2003; 2, 130 species with published abundance estimates (Hockey et al. 2005); 3, Cotgreave 1995; 4, Damuth 1991.

‡ Abbreviations are: PSN. Poisson model; MTP, metapopulation model; EXP, exponential model; NBD, negative binomial distribution model; GNBD, generalized NBD model; INBD, improved NBD model. A "+" or "−" symbol indicates, respectively, where each model passed or failed criteria.

§ LLM, log–log linear model; BEM, Bayesian estimation model.

size (Gaston and Blackburn 2000). The technique only requires a measure of species' area of occupancy at different spatial scales, and is closely linked with the calculation of detection probability and the incidence function (e.g., Hanski 1992). OAR models can predict species abundance by presupposing a specific probability distribution of population density or by assuming that particular population dynamics underlie a species distribution (He and Gaston 2000). By contrast, the second set of models is based on the scaling pattern of occupancy (SPO hereafter; Kunin 1998, Hartley and Kunin 2003, Hui et al. 2006) which describes how adjacent occupied grid cells merge with increasing grain (i.e., the percolation process of presence records across spatial scales; Hui and McGeoch 2007*a*), reflecting the scale dependence of species range size (e.g., Kunin 1998, Hurlbert and Jetz 2007). SPO models have the potential to predict species abundance by extrapolating the occupancy–scale relationship down to a scale fine enough to encompass only a single individual (Hartley and Kunin 2003). However, no tests have yet assessed the performance of SPO models at predicting species abundance from distribution data, or compared their performance to that of the OAR models. Here, the performance of six OAR and two SPO models are assessed, using data from southern African bird species.

Assessing the performance of these contending models is challenging since there are few empirical data to validate abundance estimates. Furthermore, comparing the community structure predicted by the models (i.e., macroecological patterns involving abundance data) against commonly observed patterns relies on curve fitting, which is a weak test of macroecological models (McGill 2003a). To overcome these deficiencies, we used a "dipswitch test," i.e., a combination of multiple weak tests (Rosenzweig and Abramsky 1997, McGill 2003*a*). Under such an approach, a model must pass a series of weak tests to be considered robust. Our dipswitch test comprised two classes of tests (Table 1): first, macroecological patterns associated with species abundance were derived from the models' abundance estimates, and these were compared to three well-documented patterns (i.e., three tests): the species-abundance distribution (Gaston and Blackburn 2000, McGill 2003*b*), the interspecific occupancy–abundance relationship (Holt and Gaston 2003, Blackburn et al. 2006), and the interspecific abundance–body mass relationship (Nee et al. 1991, Blackburn and Lawton 1994, Blackburn and Gaston 1996, McGill 2008). Because macroecological patterns are interlinked (Storch et al. 2008) and might simply be a by-product of a large-number network (e.g., Antoniou et al. 2002),

using just macroecological patterns for evaluating model performance cannot be considered a strong test. As a result, the second category of tests was also used. In these tests the abundance estimates for selected species were compared to independent abundance estimates in the literature (Hockey et al. 2005), and the total predicted abundance across all species was compared to abundance estimates from other regions of similar sizes (Wing 1943, Short 1979, BirdLife International 2004) (i.e., two tests). Based on these evaluations, suggestions are provided for choosing the most appropriate models under different conditions.

Methods

Eight models for estimating abundance from presence–absence maps were evaluated. The six OAR models examined included the Poisson, negative binomial, generalized and improved negative binomial, exponential and metapopulation models. The two SPO models used were the log-log linear model and the Bayesian estimation model.

OAR models

The intraspecific occupancy–abundance relationship (OAR), defined as a positive correlation between species abundance and range size (or occupancy) (Gaston and Blackburn 2000), can be used to estimate species abundance from the species occupancy. The Poisson model (PSN hereafter) has been proposed as the simplest null model of the relationship between occupancy and abundance (Wright 1991). It assumes that individuals occur randomly and independently from one another in a homogenous landscape:

$$P_a = 1 - e^{-\mu_a} \tag{1}$$

where P_a and μ_a are the occupancy and the density (or mean abundance), respectively, in samples with a grain size a (Sokal and Rohlf 1995).

Instead of assuming a random distribution of individuals, as in the Poisson model, later OAR models recognize that species distributions have a degree of spatial contagion (i.e., over-dispersion and spatial autocorrelation of population density). Over-dispersion can be caused by local dispersal within a homogenous habitat or by random dispersal in an environment with a Poisson stochastic carrying capacity (Pielou 1969), and can be described by a negative binomial distribution (Wright 1991). Based on this ecological understanding, He and Gaston (2000) suggested using the negative binominal-distribution model (NBD) to estimate abundance:

$$P_a = 1 - \left(1 + \frac{\mu_a}{k}\right)^{-k} \tag{2}$$

where k is a clumping parameter indicating the degree of over-dispersion (i.e., aggregation of individuals), ranging from $k = 0$ (highly aggregated) to the positive infinity (random, i.e., converging to a Poisson model). This NBD model is the second OAR model tested here.

The relationship between the statistical variance σ^2 and the mean abundance μ_a of the negative binomial distribution is $\sigma^2 = \mu_a + \mu_a^2/k$, from which a relationship between occupancy, density, and variance can be derived (He and Gaston 2003, Gaston et al. 2006) is as follows:

$$P_a = 1 - \left(\frac{\sigma^2}{\mu_a}\right)^{-\mu_a^2/(\sigma^2 - \mu_a)}. \tag{3}$$

This generalized NBD model (GNBD) is the third model examined here. By incorporating Taylor's power law ($\sigma^2 = c \times \mu_a^b$, with c and b being two constants) (Taylor 1961) into the NBD model (Eq. 3), He and Gaston (2003) relaxed the clumping parameter k to be scale dependent (Nachman 1981, Hurlbert 1990). From this they derived an improved NBD model (INBD):

$$P_a = 1 - (c \times \mu_a^{b-1})^{\mu_a/(1 - c\mu_a^{b-1})}. \tag{4}$$

The INBD model therefore presents a scale-free description of species distributions, and is the fourth model examined here. The successful application of the GNBD and INBD models replies on satisfying the assumptions underlying the NBD model.

Similar to the INBD model, Nachman's (1981) exponential model is also inspired by Taylor's power law. This model assumes a dynamic relationship between absence ($p_0 = 1 - P_a$) and density that can be written according to a contact process, $\partial p_0 = -g(\mu_a)p_0\partial\mu_a$, in which $g(\mu)$ is a positive function of population density. Using a contact process to model population dynamics implies an idealistic mean-field approximation, i.e., individuals are well-mixed and have equal access to all locations of the focal landscape (Hanski 1999). Influenced by Taylor and Taylor's (1977) Δ-model for explaining Taylor's power law, Nachman (1981) replaced $g(\mu)$ with a power function, leading to an exponential model (EXP hereafter):

$$P_a = 1 - e^{-\alpha \times \mu_a^{\beta}} \tag{5}$$

where α and β are two parameters. This is the fifth model examined. The general model underlying the PSN and EXP models is an occupancy-variance relationship, $P_a = 1 - e^{-\sigma^2}$, with the sample variance being replaced by μ_a and $\alpha \times \mu_a^{\beta}$ in the models, respectively. When $\alpha = \beta = 1$, the EXP model becomes a PSN model.

An alternative method to model the occupancy–abundance relationship was suggested by Hanski and Gyllenberg (1997) while discussing the link between the species–area relationship and the occupancy–abundance relationship under a metapopulation framework. They suggested a logistic relationship between occupancy and the logarithmic density, which after a simple transformation yields the metapopulation model (MTP hereafter):

$$P_a = 1 - \frac{1}{1 + \theta \times \mu_a^{\rho}} \tag{6}$$

where θ and ρ are model parameters. The metapopulation

model is the sixth OAR model examined. Previous studies have compared the performance of the six OAR models for explaining the observed forms of the occupancy–abundance relationship at different scales (He et al. 2002, Holt et al. 2002, Gaston et al. 2006, Hui and McGeoch 2007*a*), but their performances in abundance estimation have not yet been evaluated.

SPO models

The scaling pattern of occupancy (SPO) comprises the second category of abundance-estimation methods, and describes how the area occupied by a species changes across scales of measurement, i.e., the modifiable areal unit problem (Openshaw 1984). SPO models can extrapolate species abundance based on a presence–absence map using "a scale-area curve to reflect or even estimate population size by plotting or extrapolating the curve down to a sufficiently fine scale so that each occupied cell contains, on average, only a single individual" (Hartley and Kunin 2003:1565; see also Harte et al. 2001, Hui et al. 2006).

The first of the two SPO models we test is Kunin's (1998) log–log linear model (LLM). The LLM describes a power-law relationship between species occupancy and grain a:

$$P_a = \kappa \times a^{\lambda} \tag{7}$$

where κ and λ are parameters. This model assumes a fractal structure of species spatial distribution, with the box-counting fractal dimension being $D = 2(1 - \lambda)$ (Kunin 1998).

The second SPO model, the Bayesian estimation model (BEM) was developed by Hui et al. (2006). BEM only uses species occupancy at one scale but also calculates an additional index (spatial correlation, q_a) which describes the probability that the cells neighboring an occupied cell are also occupied in a binary map (Hui et al. 2006):

$$P_{4a} = 1 - \nabla^4/\Delta \qquad q_{4a} = \frac{\nabla^{10} - 2\nabla^4\Delta^2 + \Delta^3}{\Delta^2(\Delta - \nabla^4)} \tag{8}$$

where $\nabla = 1 - P_a - (1 - q_a) \times P_a$ and $\Delta = (1 - P_a)(1 - P_a^2(2q_a - 3) + P_a(q_a^2 - 3))$. BEM provides equations linking P_a and q_a with P_{4a} and q_{4a} across scales (from grain a to $4a$), with no additional model parameters. Knowing occupancy and spatial correlation at a coarse scale ($4a$), we can calculate Eq. 8 for P_a and q_a at finer scales, and thus obtain a SPO relationship. While the use of the SPO models for estimating species abundance has been suggested (Kunin 1998, Harte et al. 2001, Hartley and Kunin 2003), the performance of these models has not yet been evaluated.

Data and calculation

The presence–absence data for southern African bird species were chosen for model evaluation (Harrison et al. 1997). These data have already been used to assess species conservation status and biodiversity structure (e.g., van Rensburg et al. 2002, Hurlbert and Jetz 2007). We selected a subset of 610 species that occur in South Africa, Lesotho, and Swaziland, and excluded marine species, vagrants and (domesticated) agricultural birds (i.e., Ostrich, *Struthio camelus*, was removed because this species is commercially farmed). The atlas data were collected between 1986 and 1992, at a quarter-degree scale ($15' \times 15'$; $\sim$625 km^2), covering a total area of 1.27×10^6 km^2. Using the base resolution of the quarter-degree grid cell ($n = 1967$ grid cells) we calculated the number of half-degree ($n = 551$) and one-degree ($n = 137$) grid cells occupied by each species in a geographical information system (GIS).

Quarter-degree cell occupancy was used for the calculation of the Poisson model. For the NBD and GNBD models, quarter- and half-degree cell occupancies were used to form two equations, and μ_a and k for NBD, as well as μ_a and σ^2 for GNBD, were solved simultaneously. The three other OAR models (i.e., EXP, MTP and INBD) were solved using species occupancy at all three scales. The Newton method in Mathematica version 6.0 (Wolfram Research 2007) was used for calculations. When the problem of a Jacobian singularity arose (i.e., the Newton method might not converge, Ypma 1995), we increased the maximum iterations to 5000 and refined the initial parameter estimates. If the program still could not find a solution, no estimate was reported. For example, the metapopulation and exponential models could only estimate abundance for 14.8% and 72.8%, respectively, of species due to Jacobian singularity problems.

Parameters of the LLM model were estimated by ordinary least squares regression using occupancies at quarter-, half- and one-degree scales, and the BEM model was calculated from occupancy and spatial correlation at the quarter-degree scale. The abundance estimate of these two SPO models is reported as the number of occupied cells at the individual-area scale. To determine a "sufficiently fine" individual-area scale for estimating abundance from the SPO models, an allometric relationship between body mass (M; in kilograms, kg) and home range (H; in square kilometers, km^2) was used to determine the "individual area" of each species (i.e., the size of the home range defended by an individual; Peters 1983, Ottaviani et al. 2006). Thus, we chose to use the allometry of individual areas to calculate the "sufficiently fine scale" for estimating species abundance: for carnivores, $H = 0.6M^{0.52}$ (Peters 1983), omnivores, $H = 0.566M^{0.881}$ (Ottaviani et al. 2006), and herbivores, $H = 0.04M^{1.0}$ (Peters 1983). Data on body size and dietary requirements (49% of the 610 bird species are carnivorous; 45% omnivorous; 6% herbivorous) were obtained from Hockey et al. (2005).

Dipswitch test

Following Rosenzweig and Abramsky (1997), McGill (2003*a*) suggested using a dipswitch test as a strong

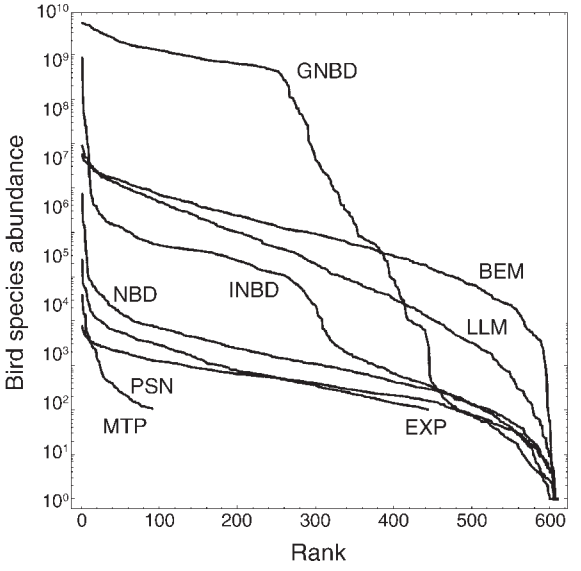

FIG. 1. Rank–abundance curves for 610 southern African bird species generated by eight models: the Poisson (PSN), metapopulation (MTP), exponential (EXP), negative binomial distribution (NBD), generalized negative binomial distribution (GNBD), improved negative binomial distribution (INBD), log–log linear (LLM), and Bayesian estimation (BEM) models. Note the log scale for abundance.

inference technique for model evaluation in macroecology. Our dipswitch test of model performance comprised a series of five independent tests with a total of 15 criteria (Table 1). In the first test, we examined if the distribution of estimated abundances conformed to the widely observed log-normal species–abundance distribution (McGill 2003*b*). Because species–abundance distributions are regularly left skewed after log-transformation (Gaston and Blackburn 2000), we also tested if the distributions were left skewed. Finally, as a third criterion, the smoothness of the rank–abundance curves was also subjectively determined, since curves that are not smooth will lead to multimodal species–abundance distributions which are rare in nature.

For the second test, the relationship between species occupancy (logit-transformed) and abundance ($\log_{10}$-transformed) was analyzed using ordinary least-squares regression (following Williamson and Gaston 1999, Holt and Gaston 2003). The resulting regression slopes were then compared to the slope observed for 183 British bird species (Holt and Gaston 2003), as well as the slope observed for the 130 southern African species for which independent abundances estimates were available (see Hockey et al. 2005).

For the third test, the abundance–body mass relationship was determined from the estimated species abundances ($\log_{10}$-transformed) using ordinary least-squares linear regression (Blackburn and Lawton 1994, Blackburn and Gaston 1996). The slope of the abundance–body mass relationship was then compared to that observed for 200 Australian bird species (Cotgreave 1995; slope $= -0.82$), the hypothesized -0.75 slope from the Damuth's rule (e.g., Damuth 1991, Nee et al. 1991, White et al. 2007, McGill 2008), and the slope observed for the 130 southern African species for which independent abundances estimates were available. The nature of the abundance–body mass relationship remains a matter of debate, both regarding the genuine slope value thereof, and the mechanisms underlying the relationship (e.g., Russo et al. 2003, White et al. 2007), which could affect the results from this test. This further emphasizes the importance of using a dipswitch test, rather than a single test, in examinations of macroecological models.

Hockey et al. (2005) provides gross estimates of population size for 130, mostly rare, species (i.e., independent abundance estimates). For the fourth test, the strength of the relationship between these independent abundance estimates (used as observations) and the predicted abundance from each model for these 130 species were assessed using generalized linear models. The MTP and EXP models were not able to predict the abundance of all 130 species (due to Jacobian singularity problems), but we still assessed their predictions as for the other models. Due to strong statistical overdispersion, the data were modelled using a quasi-likelihood approach (i.e., assuming a quasi-Poisson error structure) (Anderson et al. 1994, Richards 2008) and model significance was assessed using F tests (Collet 1991). Model selection was based on quasi-AIC values and their associated Akaike weights (Anderson et al. 1994, Richards 2008). T tests were used to test if the slope of each relationship differed significantly from 1 (a slope of 1 would indicate an unbiased prediction).

Finally, for the fifth test, the predictions of total bird abundance, summed across all species, were compared with estimates from other regions. Wing (1943) provided an abundance estimate for the birds of the United States using the Bird-Lore Christmas Censuses (now known as Christmas Bird Count by the National Audubon Society; *available online*).[6] We also extrapolated Short's (1979) estimate of the total bird abundance for the United States and southern Canada by subdividing the abundance map and summing abundance across all the cells. We also summed the estimates for 434 regularly occurring species in 25 European Union countries as an approximation of the total abundance of European birds (BirdLife International 2004). These three data sets established a baseline for the total abundance of birds at a subcontinental extent. Overall, even though each of these five tests (Table 1) was arguably weak, together they formed a strong dipswitch test of the performance of the seven models. A dendrogram from the cluster analysis was then presented, based on the performance of these eight models in the context of the above 15 criteria (Table 1), to illustrate the relative relationship between each model and an ideal model (that is, a model passing all criteria).

[6] ⟨www.audubon.org⟩

Results

Predicted community assemblage structure, as represented by rank–abundance curves (Fig. 1), differed between models. The GNBD (generalized NBD) and INBD (improved NBD) models gave curves that dropped sharply for the middle-ranking species (rankings between 260 and 460). The MTP (metapopulation) and EXP (exponential) models could not predict abundance for enough species to assess the smoothness of their rank–abundance curves. However, all the other models produced smooth curves, with the NBD (negative binomial distribution) model and the BEM (Bayesian estimation model) predicting almost parallel curves for the middle-ranking species (Fig. 1). The curve generated from the LLM model (log–log linear model) follows the curve from the BEM closely, with the BEM predicting higher abundances for rare species. The shape of the predicted abundance frequency distributions also differed between models. Predictions from the NBD ($\chi^2 = 16.2$, df = 15, $P = 0.37$), the LLM ($\chi^2 = 26$, df = 22, $P = 0.25$) and the BEM models ($\chi^2 = 27.1$, df = 17, $P = 0.06$) were not significantly different from lognormal (Fig. 2), whereas others differed significantly ($P < 0.01$). All models, except the MTP and EXP models, showed left-skewed species–abundance distributions (Table 1). Therefore, only the NBD and the two SPO (scaling pattern of species occupancy) models met all the criteria for this test.

Occupancy and predicted abundance were significantly positively related for all models, with the exception of the GNBD and INBD models (Table 2). The slope of the predicted occupancy–abundance relationship for all models differed significantly from the slope of the same relationship for British birds, with the exception of the NBD model ($P = 0.376$). Similarly, the slope of the predicted occupancy–abundance relationships for all models differed significantly from the slope of the relationship for the 130 southern African birds with independent abundance estimates. However, the LLM model, with the highest P value ($P = 0.03$), was considered not to fail this sub-test to guarantee that at least one model would meet this criterion. These results imply that, in terms of the macroecological pattern of the interspecific occupancy–abundance relationship, both classes of models performed poorly (Table 1). Indeed, none of the models passed all the criteria for this test, although the NBD and LLM models performed best.

The relationship between body mass and abundance estimates was significantly negative for all the models, with the exception of the PSN and MTP models (Table 3). The slopes of the predicted abundance–mass relationships were not significantly different from the slope of the relationship for Australian birds (slope = -0.82 ± 0.08) (Cotgreave 1995) for the LLM ($P = 0.70$) and BEM ($P = 0.35$) models (Table 3). However, the slopes derived from all the other models were significantly shallower than the slope of -0.82 (Table 3). Furthermore, the slopes derived from the LLM, BEM, and INBD models were not significantly different from the slope of -0.75 from Damuth's rule or from the slope observed for the 130 southern African bird species with independent abundance estimates (Table 3). Therefore, in terms of the abundance–mass relationship test, the INBD, LLM, and BEM models passed all the criteria (Table 1).

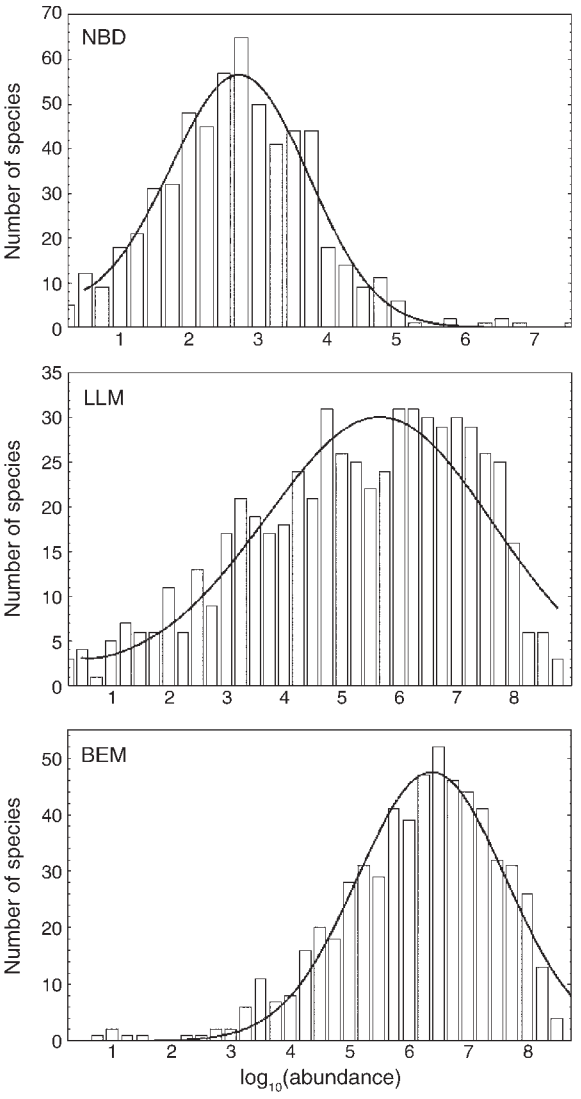

Fig. 2. Species–abundance relationships for 610 southern African bird species predicted from the negative binomial distribution (NBD), log–log linear (LLM), and Bayesian estimation (BEM) models.

Comparing the abundances predicted by the eight models and the independent abundance estimates for the 130 southern African species also showed that SPO models performed better than OAR models. Except for the MTP model, only the BEM model provided abundance estimates better than random and explained >10% of the deviance in the data (Table 4). The BEM model was clearly separated from the LLM model and

TABLE 2. Relationship between occupancy (logit-transformed) and abundance ($\log_{10}$-transformed) predicted by the eight models, together with results for the 130 southern African bird species with independent abundance estimates.

	Model statistics				Comparing regression slopes†			
					Slope = 0.66 ± 0.01		Slope = 0.27 ± 0.05	
Model	*n*	*F*	Adjusted R^2	Slope ± SE	*t*	*P*	*t*	*P*
Obs	130	35.16***	0.21	0.27 ± 0.05	8.47	<0.001		
PSN	610	43641.64***	0.99	1.12 ± 0.01	−82.82	<0.001	−18.41	<0.001
MTP	91	41.75***	0.31	−0.47 ± 0.07	15.48	<0.001	8.62	<0.001
EXP	444	103.97***	0.19	−0.48 ± 0.05	24.31	<0.001	11.43	<0.001
NBD	610	1685.96***	0.73	0.67 ± 0.02	−0.89	0.376	−8.28	<0.001
GNBD	610	0.64	0.00	0.01 ± 0.01	44.29	<0.001	5.41	<0.001
INBD	610	0.01	0.00	−0.01 ± 0.01	75.98	<0.001	5.84	<0.001
LLM	610	1054.75***	0.63	0.38 ± 0.01	24.40	<0.001	−2.20	0.028
BEM	610	551.69***	0.47	0.43 ± 0.02	12.93	<0.001	−3.11	<0.001

Notes: See Table 1 for key to the model abbreviations; *n* is the number of species; Obs indicates the independent abundance-estimate observations.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† The slope of each model is compared against the slope observed by Holt and Gaston (2003) for 183 species of British birds (slope = 0.66), as well as the slope from the 130 southern African species with independent abundance estimates (slope = 0.27).

TABLE 3. The abundance–body mass relationship ($\log_{10}$-transformed) as predicted by the eight models and as observed for the 130 southern African species with independent abundance estimates (Obs).

	Model statistics			Comparing regression slopes†					
				Slope = −0.82 ± 0.08		Slope = −0.75		Slope = −0.65 ± 0.12	
Model	*n*	*F*	Slope ± SE	*t*	*P*	*t*	*P*	*t*	*P*
Obs	130	30.52***	−0.65 ± 0.12	1.24	0.22	0.88	0.38	...	...
PSN	610	0.14	0.01 ± 0.04	9.83	<0.001	20.82	<0.001	5.38	<0.001
MTP	91	0.14	0.04 ± 0.10	6.94	<0.001	8.12	<0.001	4.49	<0.001
EXP	444	7.72**	0.11 ± 0.04	10.82	<0.001	21.99	<0.001	6.12	<0.001
NBD	610	4.28*	−0.11 ± 0.05	7.68	<0.001	12.23	<0.001	4.2	<0.001
GNBD	610	6.02*	−0.28 ± 0.11	3.91	<0.001	4.09	<0.001	2.23	0.03
INBD	610	4.53*	−0.42 ± 0.20	1.93	0.05	1.71	0.09	1.01	0.31
LLM	610	115.36***	−0.86 ± 0.08	−0.38	0.7	−1.4	0.16	−1.52	0.13
BEM	610	145.74***	−0.73 ± 0.06	0.94	0.35	0.36	0.72	−0.62	0.54

Note: See Table 1 for key to the model abbreviations; *n* is the number of species.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† The slope of each model is compared against the slope from Cotgreave (1995) for 200 Australian birds (slope = −0.82 ± 0.08), the −0.75 slope from Damuth's rule (Damuth 1991), and the slope for 130 southern African species with independent abundance estimates (−0.65 ± 0.12).

TABLE 4. Results of the regressions of predicted species abundance (from the eight models) against independent abundance estimates for 130 species.

	Model statistics						Comparing regression slopes	
Model	Null df	*F*	*P*	Deviance explained (%)	Quasi-AIC value	AIC weight†	*t*	*P*
PSN	129	3.89	0.051	3.02	68.94	<0.001	−1.88	0.06
MTP	14	8.89	0.010	63.53	6.11		0.00	1.00
EXP	100	0.00	0.954	<0.01	40.80		−1.96	0.05
NBD	129	3.09	0.081	2.40	69.35	<0.001	−2.31	0.02
GNBD	129	0.02	0.893	0.01	70.89	<0.001	−2.43	0.02
INBD	129	1.56	0.214	1.21	70.12	<0.001	−2.47	0.01
LLM	129	8.14	0.005	6.31	66.81	<0.001	−2.63	0.01
BEM	129	25.72	<0.001	19.94	57.96	0.999	−2.76	0.01

Note: See Table 1 for key to model abbreviations.

† Not calculated for MTP and EXP models due to differing sample sizes.

all OAR models by AIC weights, with a weighting of nearly 1 indicating its superiority. However, only the PSN and MTP model produced a slope that was not significantly different from 1, suggesting bias in the abundance estimates of all the other models for the 130 species (assuming that the "observed" abundances are comparatively accurate).

For the United States, the total abundance of breeding birds was estimated to be 5.66×10^9 individuals and the total abundance of wintering birds 3.78×10^9

individuals (Wing 1943). Short (1979) estimated an even higher abundance of 7.24×10^9 birds for 445 breeding species in America and southern Canada. Furthermore, BirdLife International (2004) estimated an abundance of 1.75×10^9 birds for 434 species in 25 European countries. These studies therefore set a baseline expectation of several billion (10^9) birds in the southern African region, which the PSN, MTP, EXP, and NBD models clearly fall below (estimated abundances $<0.02 \times 10^9$). The GNBD and INBD models, however, overestimated abundance, with INBD reaching 3.52×10^{12} individuals (more than 10 times the total number of birds on the planet, $1–2 \times 10^{11}$; data *available online*)[7] and GNBD predicting 1.14×10^{10} birds in the region (more than Short's [1979] prediction for North America). The two SPO models, however, estimated abundances comparable with those from North America and Europe, with 1.94×10^9 birds from the LLM model and 2.35×10^9 from the BEM model.

Comparing the performance of the models across all five tests showed that none of the models passed all the criteria (Table 1). Overall, OAR models and SPO models were clustered into two separate groups, with the ideal model (i.e., passing all criteria) belonging to the SPO group (Table 1; Fig. 3).

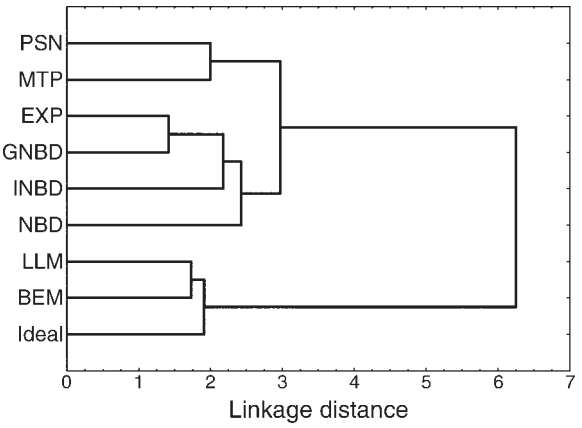

FIG. 3. A dendrogram showing the clustering of the eight models using Ward's linkage rule and Euclidean distances (based on Table 1). The "ideal" model meets all criteria. The linkage distance indicates the square root of the number of different results (i.e., passed or failed) in the dipswitch test between two models, calculated by Statistica 8.0 (StatSoft 2008). See Table 1 for key to model abbreviations.

DISCUSSION

Scaling pattern of occupancy (SPO) models performed better at predicting species abundance using presence–absence maps than occupancy–abundance relationship (OAR) models (Fig. 3). The reasons for the poor performance of the OAR models are twofold, with the first relating to the assumptions made by OAR models about species distributions and habitat heterogeneity. The PSN, NBD, GNBD, and INBD models all assume that the probability of finding x individuals in a randomly selected sample follows a Poisson or negative binomial distribution. Since these models represent random and aggregated distributions (due to local dispersal of individuals or density dependence of population dynamics) in a homogeneous landscape, predictions are likely to be inaccurate for any species that violate this assumption. Even though the GNBD and INBD models try to alleviate this problem by assuming power-law variance–mean relationships, the performance of these two models was not better than that of the other OAR models. The EXP model makes a similar assumption, presuming a well-mixed population in a homogenous landscape. However, the assumption of habitat homogeneity is unrealistic at regional scales. Recently, Conlisk et al. (2009) noted the limitation of OAR models and extended them by incorporating an additional spatial autocorrelation parameter. Even though the rationale of Conlisk et al.'s (2009) model is analogous to the BEM (Hui et al. 2006), it still belongs to the OAR model category, and its performance in predicting abundance from broadscale presence–absence data requires further investigation.

While the OAR models can incorporate the spatial heterogeneity induced by fine-scale biotic processes (e.g., local dispersal and density dependence), they neglect broadscale heterogeneity that is largely due to abiotic factors (e.g., climate and topography). Indeed, at broad scales, species ranges reflect the match between species niches and environmental conditions (Hengeveld and Hemerik 2002), but not the dynamic equilibrium of species demographic processes. Failing to incorporate environmental heterogeneity into OAR models explains the poor performance of these models in abundance estimation at broad scales. In this sense, the MTP models appear to have a clear advantage by considering a network of suitable patches (Hanski 1999). However, the metapopulation OAR model was derived from the observation of a logistic relationship between occupancy and the logarithmic density (Hanski and Gyllenberg 1997), and not directly from a metapopulation model. Therefore, it is unclear whether the MTP model incorporates environmental heterogeneity or not.

The second reason for the poor performance of the OAR models is that their predictions are sensitive to the scale at which occupancy is measured. For example, the clumping parameter k in Eq. 2 is scale dependent (Conlisk et al. 2007; also see He and Reed 2006), with k increasing with the grain size and approaching infinity. This implies that the NBD model simplifies to a Poisson model at broad scales, and explains why the NBD model underestimates species abundance from broadscale data (as observed with lower species abundance estimates from the NBD model than from the SPO models). This is in agreement with Warren et al. (2003) and He and Reed (2006) and suggests that abundance estimates

[7] ⟨www.earthlife.net/birds⟩

from the NBD model set a lower bound for estimates (Conlisk et al. 2007, He and Gaston 2007). Interestingly, while the model greatly underestimated the total abundance of southern African birds, the abundance-occupancy slope derived from the NBD model was not significantly different from that of the 183 British birds (Holt and Gaston 2003; Table 2). To increase the accuracy of the NBD model (and probably the other OAR models), He and Reed (2006) suggested that species distributions should be mapped at spatial scales that are relevant to the life history of the study species (i.e., maps with a resolution of 0.1 to 1 km). Therefore, the usage of the NBD model in practice requires extremely fine-scale presence–absence data that current atlas-type maps cannot provide. Furthermore, the correct way of calculating the model parameters (e.g., k in the NBD model; Conlisk et al. 2007), in fact, requires abundance information. As a result, using presence–absence maps at different scales to estimate model parameters and species abundance simultaneously in the OAR models is controversial (Conlisk et al. 2007, He and Gaston 2007), although there are no other alternatives when abundance data are not available (He and Gaston 2007).

The SPO models do not make these assumptions and, therefore, do not suffer from the same restrictions as the OAR models. At the regional scale, the distribution of suitable habitat and species distributions can be relatively accurately described by a fractal structure (With and King 2004, Storch et al. 2008). As a result, because the power-law form of the LLM model implies that species distributions have a fractal structure (as quantified by the box-counting dimension; Kunin 1998), this model provides an appropriate description of species distributions at the regional scale. Furthermore, Harte et al. (2001) also showed that species with self-similar (fractal) distributions can indeed yield a log–log linear relationship between occupancy and grain size (as in the LLM model). Although there is still debate about fractal methods and the self-similarity of species distributions (Halley et al. 2004, Hui and McGeoch 2007*b*, 2008), a power-law form of the LLM model clearly accounts for environmental heterogeneity at broad scales better than OAR models. In other words, the advantage of the LLM model over the OAR models is that its abundance estimates are insensitive to the scale at which occupancy is recorded.

Alternatively, the BEM model does not make any assumptions about environmental heterogeneity but provides scale-dependent species distributions based purely on the Bayesian principle (Hui et al. 2006). Since the BEM model incorporates the spatial structure of species' current distributions into predictions, it only requires data from one spatial scale (i.e., a data-efficient estimate). By doing so, the BEM model integrates environmental heterogeneity. Therefore, both SPO models bypass the assumptions of the OAR models and perform better at broad scales (Table 1).

However, while the LLM model provides accurate abundance estimates at regional scales (Hartley and Kunin 2003, Wilson et al. 2004), the fractal structure of species distributions breaks down at finer scales, causing the LLM model to yield an inappropriate spatial structure of species distribution (Hui and McGeoch 2007*c*). This occurs because at fine scales, species life-history characteristics (e.g., dispersal) are more important than habitat heterogeneity in determining the spatial nonrandomness of species distributions. Therefore, for fine-scale data OAR models should perform better than the LLM model (Harte et al. 2001). However, this does not necessarily mean that both SPO models are unsuitable for fine-scale applications. For example, the BEM model predicts occupancy equally well as the NBD model at fine scales (Hui et al. 2006).

In response to Conlisk et al.'s (2007) criticism of one of the OAR models, He and Gaston (2007:658) point out two challenges for estimating abundance from species distribution: the need to (1) "deduce spatial information from occurrence data and incorporate this into abundance estimation" and (2) "develop methods for estimating abundance across large landscapes." We respond to these challenges by proposing the SPO models (LLM and BEM), which use the spatial scaling of species distributions, for estimating species abundances at large scales. Unlike OAR models that are constrained by the assumption of environmental homogeneity and scale-dependent abundance estimations (and thus are only applicable to small homogeneous areas; He and Gaston 2007), both SPO models exploit the scale dependence of species range size and bypass the limitation of environmental heterogeneity by assuming a fractal-structure landscape for LLM or by performing a Bayesian estimation of species distribution for BEM. The scaling (scale-dependent) pattern of species distributions (Wilson et al. 2004) is thus the key to designing models for estimating abundance and explaining macroecological patterns.

The objectives of macroecology are threefold: identify, explain, and predict large-scale patterns in biodiversity. The first two objectives are normally achieved using the comparison of the best-fitting curves from different models (He and Gaston 2000), such as the power-law vs. exponential shape debate of the species–area curves (e.g., Tjørve 2003). The curve-fitting comparison also prevails in the model testing of other macroecological patterns, such as that of the species-abundance distribution (e.g., Tokeshi 1993, Hubbell 2001) and of the occupancy–abundance relationship (e.g., He and Gaston 2000, 2003, Holt et al. 2002, Hui and McGeoch 2007*a*). McGill (2003*a*) argued that the free parameters and the central-limit theorem of statistics make curve fitting a weak test in the sense that the same curve shape can be derived from multiple explanations and that the discrimination of certain models depends on the measures of fit. Our results confirmed McGill's concerns

that the use of curve fitting is on its own not sufficiently reliable to evaluate models in macroecology. However, we have to acknowledge that the dipswitch test can only assess the relative performance of each model. An absolute and direct comparison of the prediction of the dependent variable (here abundance) with empirical or observed data should still be preferred when the data allow. However, this is not currently feasible for many macroecological studies.

In conclusion, at broad scales, SPO models performed better than OAR models in estimating abundance and in deriving the subsequent macroecological patterns. OAR models should be restricted to fine-scale studies in relatively homogeneous environments, where they will theoretically perform better than the SPO models when species life-history processes and population dynamics explain the spatial structure of the species distribution. By contrast, SPO models are more suited to predicting species abundances across broad scales, and therefore their implementation and continued development may be of considerable conservation value, especially where conservation assessments and planning can be improved by the inclusion of abundance data (e.g., Gaston et al. 2001, Faith et al. 2008).

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